

NATURAL HISTORY OF SHIPWORM, *TEREDO NAVALIS*, AT WOODS HOLE, MASSACHUSETTS.

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SECTION I. OCCURRENCE.

The common species of shipworm at Woods Hole, as identified by Kofoed and Clapp, is *Teredo navalis*. The date of its first appearance in this region is not known. Verrill lists it in his "Invertebrate Animals of Vineyard Sound and Adjacent Waters" (1871). Whatever its history in American waters may have been, it is now known to occur throughout the entire North American coast from Alaska to Labrador.¹ The present study has been carried on during the past four years and in that time no other species has been collected. It is known, however, that *Bankia fimbriata* occurs in this region, although in comparatively small numbers. During the year this work was first undertaken it was difficult to obtain *Teredo* in sufficient numbers for satisfactory study, but this is not an indication that the species is not abundant in New England waters. The reason for an apparent scarcity is that shipworms are inaccessible, being, for the most part imbedded in piles and permanent structures. Subsequently, by putting out suitable timbers during one summer to be studied the next, it has been an easy matter to obtain *Teredo* in abundance. Lobster pots² and 2×4 stakes have been found to be the most convenient. If these timbers are exposed to the water during the latter part of the summer they are found to contain sexually mature worms by the beginning of the breeding season the following June. The 2×4 stakes give best results if exposed

¹ Nelson, '22, speaks of an infestation of *Teredo navalis* in Barnagat Bay, New Jersey, as a sudden outbreak. He is probably in error in thinking that this species arrived so recently on the New England coast.

² Lobster pots are constructed of small slats about the size of ordinary plasterer's lath, 2 in. broad and $\frac{1}{2}$ in. in thickness.

during July or early August, but the smaller timbers are liable to complete destruction before winter if put out early in the summer.

Teredo do not grow large in small timbers such as are used in the construction of lobster pots, but are easily removed from such small strips of wood, thereby facilitating study. The size attained depends upon the degree of crowding. To ascertain the size to which *Teredo* will grow, it is necessary to supply larger pieces of wood and 2×4 stakes are excellent for the purpose. With a drawing knife it is possible to expose the entire burrow in a few minutes because *Teredo* tunnels with the grain of the wood, usually within half an inch of the surface. A study of such stakes has shown that *Teredo* larvæ attack the wood in great numbers at the mud line but less and less abundantly from the bottom to the surface of the water. Three fourths of the *Teredo* burrows in an exposed timber occur within two or three feet of the mud line. Very few are found more than four feet above the bottom.

SECTION II. ANATOMY, PHYSIOLOGY AND BEHAVIOR.

The anatomy of *Teredo* has been accurately described by several early investigators and more recently the shell and digestive tract have received attention by Miller and Lazier, whose admirable work is published in four papers. It is sufficient here to say that the shipworm has the structure of an ordinary lamelli-branch in which the body is much elongated and in which the bivalve shell is highly modified in adaptation to the burrowing habit. In one particular my observations are not in agreement with those of Miller. He attributes the formation of the rings of growth, the rasping ridges, and denticles of the shell to alteration or fluctuation in the food supply which, according to his conception, results in corresponding periods of slow and rapid growth. This may account for the annual rings of growth of certain mollusks and has been so interpreted, but it could hardly account for the rings and ridges on the shell of this young animal which adds two rings per week in the early stages of its development. These sculpturings of the shell which adapt it to burrowing are undoubtedly due to the action of little tongues

of mantle tissue which are pushed up over the edge of the shell during deposition of the shell material. This process of shell sculpturing was observed in the large lamellibranch *Atrina rigida* (Grave, '09). The peculiar form and pattern of the shell is specific and is a matter of inheritance, but the building process is due to the peculiar manipulation of the mantle and not to alternate periods of starvation and plenty.

The physiology of digestion has been studied particularly in recent years by Dore, Miller and Potts.

Potts ('24) corroborates the work of Dore and Miller ('22) in showing that as the shipworm burrows through the wood it swallows the chips and derives some nourishment from them. A large section of the digestive tract seems to be devoted entirely to the digestion of wood (the cæcum and liver). Potts believes that wood is the only food of *Teredo* but Miller shows that the digestive tract contains diatoms as well as wood. The burrow mainly serves as a means of protection.

As the *Teredo* grows it enlarges its burrow proportionately until at maturity it may be 16 inches in length and have a diameter of $\frac{3}{8}$ of an inch (40×1 cm.). A pile or other exposed piece of timber may be honeycombed with *Teredo* tunnels without showing on the surface that it is infested. The only opening of the burrow leading to the outside is the minute pore through which the young *Teredo* entered the wood as a metamorphosing veliger. Although less than .35 mm. in diameter and therefore too small to be seen readily by the unaided eye, it is through this passage that the siphons are protruded to obtain respiratory currents and food other than wood. The shipworm feeds upon minute organisms derived from water currents that pass over its gills for respiration, just as in ordinary lamellibranchs. It is in fact an elongated lamellibranch, whose burrowing shell covers only its anterior tip, leaving most of the body and the siphons unprotected except for the wooden shell-lined burrow.

CHARACTER OF THE BURROW.

The burrows are always lined by a calcareous substance, except at the anterior end, where further excavation is taking place.

This shell-like material is secreted by the general surface of the body or mantle. It has been suggested that this lining of the burrow not only makes a smooth surface, but shuts out wood acids as well as external enemies which might otherwise injure the soft body of the animal. Even the outer pore-like opening is lined with this secretion and is divided transversely by a partition, so that the siphons protrude through two minute pores just large enough to transmit them. While the shipworm is not feeding, or when it is disturbed, the siphons are withdrawn and the external openings are plugged by two curious horny pallets, as they are called, situated one on each side of the siphonal region. See Figure I.

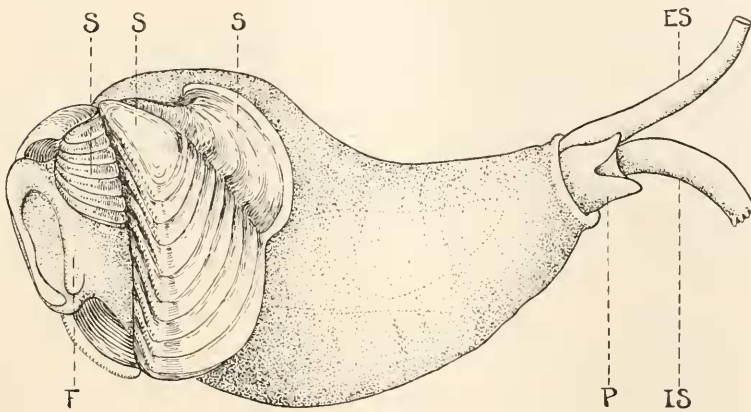


FIG. I. Young *Teredo*, length 2 cm., age five weeks from metamorphosis; drawn by camera lucida. S shell, F foot, i. s. incurrent siphon, e. s. excurrent siphon, p. pallet.

Effect of Adverse Conditions. (Repairing the burrow, etc.)

In case the tunnel is broken by accident, or by the wearing away of the surface of the wood from any cause, the adjacent glands secrete shell substance in greater abundance and mend the breach. The integrity of the burrow is carefully preserved. In case adverse conditions arise which make the environment difficult either from enemies or poisons in the water, or from overpopulation by its fellows, this shell substance is secreted in the form of a heavy casing, not only on the sides, but over the anterior burrowing end as well. This is the invariable reaction of

Teredo to adverse external conditions, the most common cause of which is the crowding of individuals in small timbers. As a consequence, the wood becomes extremely fragile, a mere shell, so porous that enemies, such as bacteria and parasitic protozoa, find entrance and menace the life of the community. Under these conditions the worms die within the first year. It may be, too, that wood is an essential part of their diet, but it is more probable that the trouble is a lack of adequate protection against adverse conditions and dangers from without.

No *Teredo* ever molests the burrow of another. When two come close together they face about and proceed in another direction, thus avoiding each other. When they become so closely crowded that further burrowing would infringe upon a neighbor, growth seems to stop. The size attained depends upon the amount of crowding. As stated above, the *Teredo* responds to these conditions by greatly thickening the shell lining of its burrow on the front as well as on the sides so that the whole is strongly encased. However, it is at best a brittle affair and parasitic protozoa and bacteria are admitted which soon destroy the occupant. The protozoan *Architophrya* (a holotrich) is always abundant in such situations.

It is difficult to see how growth may cease and the animal survive, but it is perfectly clear that *Teredo* three months old living in crowded situations are often less than one fifth as large as others of the same age growing under better conditions. The stunted worms, though packed closely together are frequently all alive and reproducing. As many as seven young *Teredo* per square inch have been observed in test blocks although the average is by no means so high. When these worms all become two or three inches long, a crowded group results unless they happened to have entered a large timber which permits of unlimited expansion.

Shipworms rarely go from one board to another, no matter how closely the boards are applied to each other. Only two exceptions to this rule have been observed among the thousands of burrows studied. They seem to avoid anything that threatens to interrupt the continuity of their tunnels.

Teredo seems not to orient to gravity since it burrows down-

ward about as frequently as upward. The burrow of a single individual often shows that there is no tropistic response of this kind. If in tunneling downward a *Teredo* approaches the end of the timber, another *Teredo* burrow or a knot, it may turn directly about and proceed in the opposite direction, paralleling the first part of its burrow. By some means it is able to detect any nearby surface of the wood and avoid it. Two *Teredo* tunnels may approach within an eighth of an inch of each other, but they remain quite separate. They have some sense also which warns them, when approaching the end of a timber, to face about before reaching the end, retreating usually at a point 5 to 10 mm. from the tip.

SECTION III. THE BREEDING SEASON.

My interest in *Teredo* dates from 1922 when the National Research Council suggested the study of the breeding season of this species and appropriated funds to meet preliminary expenses. The results of this study were reported at the Washington meeting of the American Association for the Advancement of Science in 1924, and an abstract was printed at that time. The publication of the paper as a whole was deferred until the study of various details could be completed.

The fact that the female carries the young embryos in the gill chamber for a short time makes an accurate study of the breeding habits a comparatively easy matter. It may be ascertained at a glance whether a female is carrying embryos or not and the presence of eggs or embryos in the suprabranchial chamber is conclusive evidence of recent spawning. A further useful indicator is that of color. The eggs and young embryos are pure white, but they gradually take on a dark gray color with age.

The first spawning at Woods Hole occurs from the first to the middle of May, and the last about the middle of October. During 1925 eggs were first obtained on May 15 and these were in a late cleavage stage when discovered. Two of twenty females examined had spawned at this date. In 1926 eggs were first obtained on May 16. Two of the twelve females examined had spawned, and the embryos were in the gastrula stage of development. Frequent previous examinations in April and May had shown no spawning individuals.

During the fall of 1925 and 1926 special trips were made to Woods Hole in order to determine the extreme limits of the breeding season. At this time an effort was also made to learn how late in the fall veligers were metamorphosing and entering wood. On September 22, 1926, numerous females, both in Eel Pond and at the Cayadetta Wharf in Vineyard Sound, were carrying embryos in various stages of development. On October 10, of sixty *Teredos* taken from Eel Pond, none were carrying embryos, while five of twenty five taken from the Sound had quantities of veligers in their gills. The embryos of one of these were late trochophores or early veligers and repeated observation on the rate of development in *Teredo* has shown that these would normally be carried from ten days to two weeks longer. None were found carrying embryos on November 4. These and other data show that the breeding season in Eel Pond ended two weeks earlier than in Vineyard Sound. The difference in temperature is apparently the cause of this diversity in the duration of the breeding season, Eel Pond being approximately two degrees colder during the fall than the deeper water of the Sound. Kofoid noted a similar difference in the breeding season in various parts of San Francisco Bay where wide stretches of shallow water become several degrees warmer in early spring and cooler in the fall than the deeper portions of the same body of water. His estimate of two weeks difference is no doubt conservative. Observations just completed at this writing show that the first spawning by *Teredo* in Eel Pond in 1927 occurred on May 1 and in Vineyard Sound on May 12. Spawning occurred in each case when the water had reached a temperature of approximately 11° C. (between 11° and 12° C.). Since spawning ceased in Eel Pond on October 1 and in Vineyard Sound about October 15 we have the same variation due to temperature difference and the total spawning season for *Teredo* at Woods Hole is shown to be nearly or quite five months in duration.

It should be explained that the larva has a free swimming period of approximately two weeks after leaving the supra-branchial chamber of the mother before it is ready to enter wood. In accordance with the fact that veligers are carried by the mother as late as October 20 in Vineyard Sound, one would expect to

find that wooden structures are being entered by the metamorphosing veligers until the first of November. The facts, however, do not bear out this expectation. The last date on which veligers successfully metamorphosed and attacked wood in Eel Pond was September 23, whereas larvæ were no doubt present until about October 5. Lobster pots placed in Vineyard Sound on October 10 were entered by metamorphosing veligers. It is certain that larvæ are present in the water in Vineyard Sound until November 1 or the last week in October. In other words, larvæ are present in the water at least two weeks after the last ones successfully attack wood. The reason for this is not evident. The cilia of the swimming mechanism of the larva possibly become less and less active as the water cools, with the result that mortality among the last generation of larvæ of the season is high. In *Bugula* also the last larvæ of the season fail to metamorphose, but not to so great an extent as is the case with *Teredo*.

An examination of the gills of a large number of *Teredo* on November 4 showed a spotting of these organs as if the last embryos contained had been resorbed. It is quite likely that the belated ones lose ability to swim and therefore remain inactive and disintegrate in the gill chamber. (This may not be the correct explanation of the cause of the failure of the last embryos of the season to metamorphose.) The larvæ of *Bugula* and those of certain hydroids continue to metamorphose successfully into November and the latter into December although dependent upon cilia for locomotion.

The data in hand indicate that the breeding season of *Teredo* at Woods Hole extends from about May 10 to October 10 or possibly to October 15, a period of five months.

Fecundity.

Teredo is tremendously prolific. Each female spawns three or four times in a season. The number of eggs produced varies with the size of the individual and is estimated to be from one to five millions. At the end of the season the female seems to be exhausted. Many molluscs survive for several years but *Teredo* dies during the second year as test blocks have shown repeatedly. This unusual fecundity may explain the early loss of vitality.

As evidence that the female *Teredo* spawns every four or five weeks, the following data are offered. Several cases of this kind were observed.

June 20, 1925. Two large females which were carrying gray veligers, were ready to spawn a second time. The ovaries were large and distended with eggs which were full size and fertilizable.

June 24, 1925. Two among several females examined had spawned a second time this season, numerous late veligers mixed with cleaving eggs were found in the suprabranchial chamber.

Periodicity.

One of the specific objects of this study was to ascertain the characteristics of the breeding season, whether or not there is a lunar or other periodicity in the production or shedding of the gametes. It was made apparent during the first year's study that no lunar periodicity occurs in the spawning of *Teredo*. From the beginning to the end of the breeding season, the water contains abundant larvæ in all stages of development. The records of examinations of hundreds of stakes and lobster pots indicate that larvæ are abundant in the water ready to attack any exposed timber each day of the summer. The evidence bearing on this point is derived from two types of experiments which are here described in some detail because other workers have stated that the spawning of *Teredo* is periodic and that definite broods mature at definite times.

1st. The following tables show that no periodicity in the spawning by this species occurs. Of a large number of ship worms that may be examined at any time during the summer, some will be found to carry cleaving eggs, some gastrulæ, and some trochophores, some young veligers and some typical veligers, thus showing that spawning is continuous and not synchronous.

TABLE I.

Teredo EXAMINATIONS 1925, JULY 1.

Material from Lobster Pot Placed in Water Aug. 16, 1924. Ecl Pond.

Females carrying unspawned eggs	4
Females carrying cleaving eggs in gill chamber	1
Females carrying young veligers in gill chamber	1
Females carrying typical veligers in gill chamber	4
Mature males with active sperm	7
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Total	17

TABLE 2.

Teredo EXAMINATIONS 1924, JULY 5.*Material from Lobster Pot Placed in Water Aug. 20, 1923. Cayadetta Dock.*

Females carrying mature eggs	5
Females carrying immature eggs	1
Females carrying cleaving eggs in gill chamber	7
Females carrying gastrulæ in gill chamber	5
Females carrying young veligers in gill chamber	4
Females carrying typical veligers in gill chamber	5
Mature males having motile sperm	7
Immature males	3
Total	37

TABLE 3.

Teredo EXAMINATIONS 1924, JULY 19.*Material from Lobster Pot Placed in Water Aug. 20, 1923. Cayadetta Dock.*

Females carrying eggs	8
Females carrying cleaving eggs in the gill chamber	2
Females carrying gastrulæ in the gill chamber	11
Females carrying young veligers in the gill chamber	3
Females carrying typical veligers in the gill chamber	5
Mature males with active sperm	5
Total	34

TABLE 4.

Teredo EXAMINATIONS 1924, AUG. 10.*Material from Lobster Pot Placed in Water Aug. 20, 1923. Ecl Pond.*

Females carrying eggs	1
Females carrying cleaving eggs in the gill chambers	1
Females carrying blastulæ or gastrulæ	4
Females carrying early veligers	2
Females carrying typical veligers	5
Females carrying a few veligers in the gill chambers, apparently spent	1
Mature males with abundant active sperm	12
Total	26

These four tables show that spawning takes place at all times during the month and not synchronously. They show conclusively that there is no lunar or other periodicity such as that sometimes caused by variations of temperature. Attention is

called to the fact that the spawning of these animals took place not in the laboratory, but normally in their natural habitat.

It is also apparent from these tables that there are no "broods" or special times of infestation of exposed timber. As further evidence on this point the test blocks (lobster pots) were put out every ten days during the summer and all became infested with metamorphosing *Teredo* larvæ almost at once, certainly within a day or two after exposure, as numerous experiments on rate of growth show. At Woods Hole the first larvæ settle and begin to burrow toward the end of June (June 20). From that time on until early fall the water contains a copious supply of swimming larvæ ready to burrow into any exposed wooden structure.

T. C. Nelson in his report for the year 1923, Table 5, page 208, concludes on very meager and insufficient data that one brood of larvæ settled in Barnegat Bay in June and that a second brood matured some time between July 26 and September 4. The evidence derived from my experiments covering four years show that there are no broods but rather a continuous entrance of timbers by larvæ maturing throughout the breeding season. The evidence of many experiments shows that one can not depend upon green timber or even seasoned 2×4 stakes for such experiments, as they may remain uninfested for weeks for no apparent reason. Seasoned lobster pots, however, regularly became infested either the day they were exposed to the water or very soon thereafter. This is possibly due to the horizontal position of the timbers in the water, as contrasted with stakes standing vertically. The answer to the question whether *Teredo* larvæ enter wooden structures in broods at special times or continuously has important practical bearings as well as scientific interest.

It is also apparent from the data of these tables that Nelson's statement that there are five hundred females to one male, does not hold for the Woods Hole region. Females outnumber males but by no means to so great an extent.

Kofoed has shown that the number of larvæ in any particular region depends upon the extent to which infested timber is present. Regions far from wooden warves have relatively few larvæ in the water. I was able to show that *Teredo* is much more abundant at the Cayadetta Wharf than in Eel Pond, the

ratio being approximately 2:1. The distance between these locations is less than one hundred yards and the difference in numbers in this case is not due to a difference in the amount of wood present. The biological conditions in the more or less isolated Eel Pond are clearly different from those of the open waters of Vineyard Sound because species inhabiting them are different to some extent, as shown in another paper (See *Bugula*).¹ A study of these conditions is contemplated but at the present no adequate explanation is suggested unless the large amounts of formalin and other poisons and oils from the supply station seriously affect the Eel Pond water at times. There are, however, differences in natural conditions. The tidal currents outside, at any rate, are much stronger than those in Eel Pond.

SECTION IV. EMBRYOLOGY, AND RATE OF DEVELOPMENT.

The extensive contributions of Sigerfoos and Hatschek give satisfactory descriptions of embryological development so that I shall avoid duplication and emphasize only facts that are new.

The egg of *Teredo* is comparatively small and white in color. It measures in extreme limits from .050 mm. to .061 mm. with an average diameter midway between these figures. The oviducts open into the suprabranchial chambers which are extensive and serve as brood pouches. When the eggs are extruded they are retained in the suprabranchial chambers for a period of two or three weeks, during which time they pass through the early stages of development. When liberated into the sea water they are typical lamellibranch veligers, vigorous and hardy. A large female may liberate from 500,000 to 1,000,000 eggs at a single spawning, so that the gill chambers are tightly packed with embryos distributed in two parallel rows along the sides of the slender elongated body. The approximate age of embryos can be estimated by their color since they gradually change from white to a dark muddy gray during development.

The embryo is not parasitic upon the mother, but the egg will not develop outside the gill chamber. Ripe eggs were several times removed from the gonads and artificially fertilized in an

¹ *Bugula flabellata* lives readily in Eel Pond but will not thrive in the adjacent waters of Vineyard Sound, while the reverse is the case with *B. turrita*.

attempt to observe them in development. Development was initiated but no egg cleaved beyond the sixteen cell stage, and many stopped at the two, four, and eight cell stages. Development in these cases was extremely slow and cleavage was irregular and abnormal. Eggs fertilized at six P.M. had reached the eight cell stage at 9 P.M. It is probable that development in this species is normally slow, but this rate can hardly be considered normal. Very young embryos in the two and four cell stages were several times found in the suprabranchial chambers and these when removed developed no better than the artificially fertilized eggs. In common with artificially fertilized eggs, they finally became viscid and adhered to the containing dish. It was found also that blastulæ and gastrulæ would fare no better. They failed to develop into swimming larvæ. Late trochophores and early veligers on the other hand continued to develop normally when removed from the gill chamber to sea water. Veligers removed prematurely showed great vigor and swimming ability, and were several times kept for two weeks in sea water. Veligers withstand much rough treatment and survive in poorly aerated and even foul water. Some were kept in glass aquaria and fed on diatoms for three weeks, but to what extent they metamorphosed and entered the wood that was provided was not learned.

The gastrula is invaginate, similar to that of many other molluscs and annelids that produce small eggs with little yolk. The trochophore is especially interesting because in adaptation to its parasitic mode of life, it fails to develop a strong protroch. The cells which normally develop this larval swimming organ are undoubtedly present and distributed in a broad equatorial band similar to that of many molluscs, and they are more extensive than in most annelids. The protroch is apparently present and was described by Hatscheck. I found it either absent or so feebly developed as to be easily overlooked. The trochophore is pear shaped or slightly elongated and on the average measures $.059 \times .060$ mm. in length. As it begins to transform into the veliger, strong cilia develop on the velum, and the embryo becomes motile long before it is ready to be expelled into the sea water to shift for itself.

Duration of Larval Period.

Sigerfoos failed to find free swimming veligers in the water and both he and Nelson speak of the habits and duration of the larva as being unknown. The larval period from fertilization to metamorphosis has usually been estimated at about one month. It is evident, however, that it varies somewhat with temperature being shorter in tropical and sub-tropical regions than at Woods Hole.

I have frequently found *Teredo* veligers, in various stages of development, settling upon horizontally placed boards and Nelson has more recently taken them in "tow," as well as hovering about piles ready to settle permanently. In fact, he corroborates the observations of Harrington that the mature veligers of *Teredo* are attracted to wood and wood extracts. The duration of the free swimming period has never been accurately determined. To give attention to this phase of the life history publication of this paper has been delayed until its study could be completed and verified. The evidence now at hand indicates that the entire developmental period from egg to metamorphosing larva, is about five weeks. At least half of this time is required for development in the gill of the mother, leaving for the free-swimming period not to exceed two or three weeks. The evidence on which this conclusion is based is derived in various ways but is indirect. Since the method and conclusion may be questioned, the data are explained in considerable detail in the following pages.

In 1925 the first eggs were laid between May 12 and May 15, while the first young metamorphosed *Teredo* were found in test blocks on July 2 and July 5. These young, metamorphosed shipworms measured .35 mm. to .5 mm. Evidence collected from many experiments carried out during the past two years shows that young *Teredo* of this size have spent from 15 to 18 days in the wood, or rather, that they settled and began to metamorphose and burrow 15 to 18 days previously. If we subtract 15 days from July 2 or 18 days from July 5, June 17 is the approximate date when these *Teredo* ended their careers as free swimming larvæ. Other young *Teredo* collected on July 7 measured 1 mm. and these are known to be three weeks old, or that three weeks

had elapsed since they settled upon wood. Subtracting twenty-one days from July 7 gives the date June 17 when metamorphosis began. The total larval period is therefore between four and five weeks. Other data collected during 1925 lead to the belief that the time is more nearly five weeks than four. This method, though indirect, is accurate, and was repeated many times at the opening of the breeding seasons of 1925 and 1926. The experiments made to determine the rate of the metamorphosis and rate of early growth were also repeated many times during the past two years and are also reliable. They show conclusively that young *Teredo* which measure one millimeter are approximately three weeks old. The spring of 1925 opened unusually warm, although the winter was severe, so that animals came out of winter hibernation a few days earlier than usual. The effect of this was shown most markedly in the rapid somatic growth of many animals, but it also affected to a slight extent the breeding seasons of most animals. The date of first settling of *Teredo* larvæ at Woods Hole is usually about June 20, and the first spawning about May 10. The variation in the spawning season from year to year does not usually exceed two or three days but it may vary more than a week. There is evidence that some animals begin to breed only when the water rises to a certain temperature. This, however, is by no means a universal rule.

Rate of Growth.

The veliger of *Teredo* has the typical form common to lamelli-branch larvæ, but is not so thick or nearly spherical as sometimes described. Young veligers taken from the gills in an early stage of development measure on the average .065 x .080 mm. Five specimens taken from two individuals measured as follows: .060 x .080 mm.; .065 x .080 mm.; .065 x .082 mm.; .070 x .083 mm.; .070 x .085 mm. These measurements represent the range of variation in length and breadth. One of these seen in edge view measured .082 x .05 mm., and an older one .09 x .05 mm. Veligers ready to begin their free swimming life, after spending two or three weeks in the gill of the mother, measure somewhat larger, as the following examples show: .070 x .090 mm.; .072 x .090 mm.; .075 x .085 mm.; .075 x .088. These measure-

ments not only indicate some growth but also that a considerable variation exists in the relative measurements. The range of variation in ratio of length to breadth and also in length of hinge line is great. Veligers fed upon diatoms for one week measured from .077 x .090 mm. to .081 x .093 mm. The size attained at the time of metamorphosis was not learned, but Nelson ('23) gives it as .25 mm. in length. I have collected several hundred young metamorphosing *Teredo*, which had burrowed into wood, varying in age from two to three weeks after settling. These range in size from .35 mm. to 1 mm. The smaller ones in two weeks have almost completed metamorphosis and have from two to three rasping ridges or rings of growth on the shell. Individuals three weeks old have four rings of growth and a typical *Teredo* shell. At three weeks of age the *Teredo* is practically spherical and its burrow, when exposed by cutting away the surface of the wood, is a hemispherical pit. The young worm now begins to elongate rapidly and at the end of one month its burrow measures from 5 to 7 mm. in length, and has a diameter of 2 to 2.5 mm. The shipworm when expanded fills its burrow so that, in measuring the rate of growth, the size of the burrow may be taken as the correct measure of the enclosed worm. When the shipworm is removed from its burrow, it contracts to one half or two thirds of its expanded measure. Tables 5 and 6 show the rate of growth from the egg to adult size, and need not be described in detail. Measurements were taken every three or four days, and the rate of increase in size from day to day was found to be surprisingly rapid.

It should be noted that the ages given in the tables include only the time that elapsed from the time of settling. If the age from the egg is desired, about thirty-five days should be added to these figures to include the time from fertilization to the end of the free swimming period. The larval period is excluded in the following description and from the tables.

Growth during the first twenty-five days seems small but when the minute size of the animal at the beginning is taken into account, the growth is not slow. From one month to five months the increases shown during the intervals of three or four days, between measurements, are seen to be remarkably great. For



TABLE 5.

RATE OF GROWTH OF *Teredo navalis* (SUMMER).

Measurements of the Largest Burrows of Specified Ages.

Date and Period of Growth.	Age.	Size of Burrows in Length and Widest Diameter (Metric).	Approximate Length in Inches.
July 16 to July 26....	10 days	No visible <i>Teredo</i> burrows.	
July 16 to Aug. 3....	18 "	No visible <i>Teredo</i> burrows.	
July 26 to Aug. 13....	18 "	.35 to .5 mm. x .35 to .5 mm.	.014 to .02 in.
July 16 to Aug. 8....	23 "	.35 to .5 mm. x .35 to .5 mm.	.014 to .02 in.
July 16 to Aug. 11....	25 "	.5 to .1 mm. x .5 to 1 mm.	.02 to .04 in.
July 26 to Aug. 20....	25 "	1 to 1.5 mm. x 1 to 1.5 mm.	.04 to .06 in.
July 16 to Aug. 13....	28 "	2 to 3 mm. x 1 to 2 mm.	.08 to .12 in.
July 16 to Aug. 16....	30 "	5 to 7 mm. x 2 to 2.5 mm.	.2 to .28 in.
July 16 to Aug. 18....	33 "	8 to 10 mm. x 2 to 3 mm.	.32 to .4 in.
July 16 to Aug. 23....	38 "	14 to 17 mm. x 3 mm.	.56 to .7 in.
July 16 to Aug. 28....	43 "	35 to 45 mm. x 4 mm.	1.4 to 1.8 in.
July 16 to Sept. 1....	46 "	50 to 57 mm. x 4 to 4.5 mm.	2 to 2.3 in.
June 20 to Aug. 20....	60 "	70 to 75 mm. x 4 to 4.5 mm.	2.8 to 3 in.
July 3 to Sept. 6....	65 "	80 to 90 mm. x 4 to 4.5 mm.	3.2 to 3.6 in.
June 22 to Sept. 3....	72 "	100 to 120 mm. x 4.4 to 4.8 mm.	4 to 4.8 in.
June 22 to Oct. 20....	130 "	140 to 170 mm. x 6.5 to 7 mm.	5.6 to 6.8 in.
June 22 to Dec. 1....	160 "	175 to 200 mm. x 7 to 7.5 mm.	7 to 8 in.
July 1923 to July 1924	One year	250 to 400 mm. x 7.8 to 9.4 mm.	10 to 16 in. x $\frac{5}{16}$ to $\frac{3}{8}$ in.

Note.—The left hand columns of Tables 5 and 6 represent the time of exposure of timber to the sea water. Thus, if we consider the first item of Table 5, timbers were exposed to sea water on July 16 and examined for *Teredo* on July 26, making ten days as the maximum age of the infesting *Teredo* as indicated in the second column of the table. Column three gives the measurements of the infesting *Teredo* if any.

The measurements given in these tables are actual cases and not averages. Many more were measured than are given here but the data given are considered typical.

In all cases the larval period is omitted. The age from fertilization may be approximated by adding thirty-five days to the age as given here.

Timbers exposed forty-three days, July 16 to August 28 contained sexually mature worms. Other similar data show that *Teredo* under favorable conditions becomes sexually mature in six weeks at Woods Hole. The item second from the bottom of Table 5 shows that *Teredo* does not reach adult size during the first season (June 23 to December 1). No growth takes place after December 1. (See also Table 6.) The last item of the table shows that adult size is attained in one year (July 1923 to July 1924). The largest specimen found at Woods Hole measured forty centimeters in length. It was precisely one year old.

example, the length of the largest burrows at twenty-five days is 1.5 mm., at thirty days 5 to 7 mm., at thirty-eight days 14 to 17 mm., at forty-three days 35 to 45 mm. Davenport claims that

growth in size is partly due to swelling by the absorption of water. It is easier to account for this phenomenal growth in this way than to suppose that the change in size represents only protoplasmic growth and actual cell multiplication.

It has been repeatedly found that *Teredo navalis* at Woods Hole reaches sexual maturity and spawns from six to eight weeks after entering the wood as a metamorphosing larva. The youngest to spawn were six weeks old, and their burrow measured one and one half inches (38 mm.) in length. They spawned in abundance at the age of two months when they measured 2-2½ inches (50 to 63 mm.) in length. Sexual maturity is reached long before adult size is attained, since a fully developed shipworm measures from 12 to 16 inches (30 to 40 cm.) in length.

The larvæ that metamorphose first in a season almost reach adult size by December 1, the largest ones, measuring from seven to nine inches (17.5 to 22.5 cm.) in length. During December, January, February and early March ship worms are practically dormant and do not grow perceptibly. Then they may be said to awaken and by the first of July the oldest have reached maximum size. The largest specimen found at Woods Hole measured 16 inches in length and ¾ inch in widest diameter (40 x 1 cm.). It grew in a 2 x 4 test take which was in the water from July 1, 1923 to July 1, 1924. Others measuring from 12-15 inches are common. Larvæ which enter the wood later in the summer, even to October 1, lie dormant over winter and resume growth the following spring. It was shown that growth is greatly retarded after the first of November, especially on the part of the youngest *Teredo*. Table 6 shows the rate of growth for the entire year including the winter. It has already been stated that *Teredo* reaches adult size in one year and dies during the second year.

Teredo navalis is said to grow to a slightly larger size in sub-tropical climates than at Woods Hole. As stated above the largest specimen found in this northern locality in four years' study measured forty centimeters in length and one centimeter in greatest diameter.

TABLE 6.
RATE OF GROWTH OF *Teredo navalis* (EFFECT OF WINTER UPON GROWTH).
Measurements of the Largest Burrows of Specified Ages.

Period of Growth or Time of Exposure of Timber.	Age.	Size of Burrows in Length and Widest Diameter (Metric).	Length and Width of Burrows in Inches.
Nov. 1 to Dec. 1.....	1 month	No teredo infestation.	$1\frac{1}{4}$ to $1\frac{3}{4}$ in. x $\frac{5}{32}$ to $\frac{3}{16}$ in.
Oct. 15 to Dec. 1.....	$1\frac{1}{2}$ "	No teredo infestation.	3 to $3\frac{1}{4}$ in. x $\frac{1}{16}$ to $\frac{1}{32}$ in.
Oct. 1 to Dec. 1.....	2 "	No teredo visible.	4 to $4\frac{1}{16}$ in. x $\frac{1}{4}$ to $\frac{1}{32}$ in.
Sept. 15 to Dec. 1.....	$2\frac{1}{2}$ "	No teredo visible.	$4\frac{1}{2}$ to $5\frac{3}{4}$ in. x $\frac{1}{4}$ to $\frac{9}{32}$ in.
Sept. 1 to Dec. 1.....	3 "	No teredo visible.	6 to $8\frac{1}{2}$ in. x $\frac{1}{4}$ to $\frac{3}{32}$ in.
Aug. 20 to Dec. 1.....	$3\frac{1}{2}$ "	35 to 45 mm. x 4 to 4.5 mm.	7 to 10 in. x $\frac{1}{4}$ to $\frac{3}{32}$ in.
Aug. 10 to Dec. 1.....	$3\frac{3}{4}$ "	75 to 81 mm. x 4.5 to 5 mm.	10 to 16 in. x $\frac{1}{16}$ to $\frac{5}{8}$ in.
Aug. 1 to Dec. 1.....	4 "	100 to 110 mm. x 6.2 to 7 mm.	$1\frac{1}{16}$ to $2\frac{5}{8}$ in. x $\frac{1}{8}$ to $\frac{1}{6}$ in.
July 20 to Dec. 1.....	$4\frac{1}{4}$ "	112 to 144 mm. x 6.2 to 7 mm.	$\frac{1}{2}$ to $\frac{5}{8}$ in. x $\frac{1}{16}$ to $\frac{3}{8}$ in.
July 10 to Dec. 1.....	$4\frac{3}{4}$ "	159 to 210 mm. x 6.2 to 7 mm.	
July 1 to Dec. 1.....	5 "	175 to 250 mm. x 6.2 to 7 mm.	
July 1 to Dec. 1.....	12 "	250 to 400 mm. x 7.8 to 9.5 mm.	
Sept. 12 to July 1.....	Winter +	48 to 70 mm. x 3.3 to 4.1 mm.	
Sept. 23 to July 1.....	Winter +	12 to 31 mm. x 2.5 to 3.3 mm.	

Note.—Table 6 shows, primarily, the amount of growth attained by *Teredo* during the first season up to the beginning of the hibernation period (Dec. 1). It shows not only that the earliest larvæ of the season fail to reach maturity (adult size) the first season, but also gives the amount of growth attained by the later larvæ of the season as well.

The first five items of this table show that *Teredo* larvæ which enter the wood after September 1 will not attain sufficient size to be detected in the wood up to December 1. Timbers exposed to the water as late as August 20 on the other hand are likely to contain *Teredo* measuring 35 to 45 mm. in length by the end of the growing season (Dec. 1).

The last two items of the table show that timbers exposed to the water between Sept. 12 and Sept. 23 become infested by *Teredo* and that they appear in the wood the following July, although they remain too small during the winter to be detected.

The latest infestation observed at Woods Hole occurring in Eel Pond was Sept. 23, and in Vineyard Sound Oct. 10. It may sometimes occur somewhat later than this, since the point was not sufficiently investigated. Table 6 shows that growth in the late fall is very slow compared with summer growth as given in Table 5 and data not tabulated show that practically no growth takes place in *Teredo* at Woods Hole between Dec. 1 and March 1. Some observations indicate that the gonads begin to proliferate extensively before there is detectable body growth in the spring.

SUMMARY.

Teredo navalis occurs in abundance at Woods Hole and vicinity and has been known there for many years.

The breeding season extends from about May 10 to October 10. Spawning begins in the spring when the water reaches a temperature between 11° and 12° C. Spawning by each female occurs several times during the season. No lunar periodicity in spawning occurs and there are no broods caused by synchronous spawning.

The eggs are retained in the gills of the mother during cleavage and early larval development.

The time required for the fertilized egg to complete larval development to metamorphosis is approximately five weeks at Woods Hole. About half of this time is passed in the brood pouch and half as a free swimming veliger.

When eggs and early embryos are removed from the gills they do not develop normally.

The trochophore of *Teredo* is non-motile, having either a feebly developed protroch or none.

Teredo navalis reaches sexual maturity in six weeks or two

months after metamorphosis when it measures four or five centimeters in length. It reaches adult size in on year, and dies during the second year. The largest specimen collected in four years measured forty centimeters in length and one centimeter in greatest diameter.

The rate of growth during the summer months and also during the winter was determined and tabulated. Certain habits of shipworms were also observed and recorded.

APPENDIX.

Practical Measures.

Because of numerous inquiries by lobstermen and owners of small boats concerning methods of preventing damage by shipworms, a series of experiments was made on the effect of drying upon *Teredo*. These experiments were not extensive but sufficient to show that simple but effective precautions may be taken.

Teredo larvæ first begin to enter wood between June 20 and June 25 and stop about October 10. Shipworms do not enter wood at any other time during the year. Little or no damage is done to wood until it has been in the water one full month. The largest of the young shipworms are only one fourth of an inch long at the end of one month but they attain a length of one inch in six weeks. It is, therefore, advisable to dry lobster-pots and boats once per month and leave them out of the water exposed to the sun for one week. This is especially true in July and August when most of the damage is done. Shipworms in small timbers are killed by five days' exposure to sunlight, but 2 x 4 stakes and larger timbers require from a week to ten days for drying sufficiently to kill all of the worms.

EXPERIMENTS.

(1) Infested lobster-pot lath:

- (a) After exposure in air to bright sunlight for 1 day, seemed to be dry but some of the infesting shipworms were still alive.
- (b) After exposure in air to bright sunlight for 2 days, some shipworms alive.

- (c) After exposure in bright sunlight for 3 days, all shipworms dead.
- (2) Infested lobster-pot lath:
- (a) After 7 days on shelf in laboratory, all worms contracted and shrunk, some of which regained plumpness and normal activity when placed in sea water. Spermatozoa and larvæ taken from these shrunk worms showed activity.
- (b) After 10 days on shelf in laboratory—all worms, sperm and larvæ dead.
- (3) Infested 2 x 4 stakes:
- (a) After exposure in air to sunlight for 5 days; many shipworms dead, some living.
- (b) After exposure in air to sunlight for 7 days; all shipworms dead.
- (4) Infested 2 x 4 stakes:
- (a) After exposure in air in shade for 7 days; many worms dead but some living.
- (b) After exposure in air in shade for 10 days; none living.

Note.—If infested 2 x 4 stakes are exposed in air in the shade but kept wet some worms may live for several weeks.

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